

AN OVERVIEW OF THE ORIGINS OF THE MODERN VEGETATION AND FLORA OF THE NORTHERN ROCKY MOUNTAINS¹

JACK A. WOLFE²

ABSTRACT

The present flora of the northern Rocky Mountains has diverse origins. The Late Cretaceous mesothermal to megathermal evergreen vegetation of this region had few taxa, even at the familial level, that live in the northern Rocky Mountains today. The terminal Cretaceous event resulted in broad-leaved deciduous taxa occupying mesothermal climate in the northern Rocky Mountain region, where they underwent major diversification. The early Eocene thermal maximum severely restricted the areas of microthermal climate and created a climatic/geographic bottleneck for microthermal lineages. By the early middle Eocene, volcanic uplands that supported microthermal coniferous forests of Pinaceae and Cupressaceae had developed in parts of the northern Rocky Mountain region. These Eocene coniferous forests contained a diverse broad-leaved subsidiary element, most of which represented adaptive radiations of mesothermal clades into newly created microthermal climate. During the later Eocene, microthermal vegetation was progressively enriched by internal diversification and by adaptation of mesothermal groups to microthermal climate; extinction also was a major factor in the changing composition of the microthermal flora. The Eocene volcanic uplands of western North America played a major role in the diversification of arcto-tertiary clades; dispersals between western North America and Eurasia of members of these clades was readily accomplished during the later Eocene by way of Beringia. Some of the Eocene microthermal lineages survive relatively unchanged in the northern Rocky Mountains today, and other extant lineages, although ultimately derived from taxa in the Eocene uplands, represent morphological types that originated and diverged in Eurasia, arriving in North America by migration. Oligocene and Neogene floras are largely unknown in the northern Rocky Mountains, although the Columbia Plateaus to the west contain many assemblages of these ages. These assemblages represent microthermal broad-leaved deciduous or coniferous forests, and most constituent taxa represent lineages that were derived from Eocene upland vegetation following the terminal Eocene temperature deterioration. With the presence of many extant northern Rocky Mountain lineages, the Columbia Plateaus assemblages provide evidence that the northern Rocky Mountain region was probably occupied primarily by coniferous forest during the Oligocene and most of the Neogene. During the mid-Miocene thermal maximum, numerous microthermal lineages were exchanged between western North America and Eurasia. Other extant northern Rocky Mountain lineages are known during the Miocene only in areas such as Alaska and probably represent migrants into the northern Rocky Mountains during the late Neogene. The present flora of the northern Rocky Mountains therefore clearly represents a complex overlay of numerous historical biogeographic patterns.

The modern vegetation of the northern Rocky Mountain region is primarily steppe at low altitudes and coniferous forest at higher altitudes (Habeck, 1987). Temperatures are entirely microthermal.³ The lower and drier part of the coniferous forest belongs to the *Pinus ponderosa* zone, whereas most of the mesic coniferous forest at higher altitudes belongs to the *Abies grandis* zone (Franklin & Dyrness, 1969). The vegetational/climatic types that have occupied the northern Rocky Mountain region are docu-

mented by successive microfossil and megafossil plant assemblages. In some instances, lack of assemblages that represent particular intervals makes it necessary to infer climate and vegetation from the fossil record of adjacent regions. This report addresses vegetational (physiognomic) types that have occupied the northern Rocky Mountain region in the past and the history of the lineages that comprise the modern flora. Throughout, the focus is primarily on the woody flora.

¹ For many helpful discussions, I thank H. E. Schorn, G. R. Upchurch, Jr., and Wesley Wehr. Schorn has also supplied data from his unpublished studies on the affinities of many western American Tertiary conifers. P. R. Crane and B. H. Tiffney offered useful comments on the manuscript.

² Paleontology and Stratigraphy Branch, MS-919, U.S. Geological Survey, Federal Center, Denver, Colorado 80225, U.S.A.

³ Microthermal = mean annual temperature <13°C, mesothermal = mean annual temperature 13–20°C, megathermal = mean annual temperature >20°C.

The extant woody flora is composed of 10 genera and 19 species of conifers and 30 genera and 80 species of woody dicotyledons. The dominant conifers are *Abies grandis*, *Larix occidentalis*, and other members of Pinaceae, as well as a few members of the Cupressaceae. The dicotyledons are primarily adjuncts in coniferous forest or form streamside communities. Conspicuous dicotyledonous families, as elsewhere in Northern Hemisphere vegetation, include Betulaceae, Ericaceae, Salicaceae, Rosaceae, and Caprifoliaceae, with a few Aceraceae.

The origins of the flora of a region such as the northern Rocky Mountains are, of course, highly complex. Each component species, genus, and family has a unique history, although some histories may approximate others in space and time. Indeed, the search for patterns to which numerous histories approximately conform is a primary concern of historical plant geography. Such patterns might be indicative of similar responses to specific historical factors, particularly responses to environmental changes, including various parameters of climate and topographic changes resulting from orogenic factors. However, because two taxa are now in association or have similar present distributions does not imply similar histories.

The classical methodology for determining the histories of biogeographic patterns involves reconstruction of phylogenies from phenetic similarities of extant and fossil taxa, observing distribution patterns of extant taxa, and determining the patterns of distribution of fossils in time and space. The relative completeness of the fossil record is the major problem in using it in biogeographic analyses. The problem is underscored in the present case by the almost total absence of Oligocene and Neogene assemblages of plant megafossils in the northern Rocky Mountains. Although some palynomorph assemblages fill this gap, the typical taxonomic resolution of palynological morphology is typically at a generic or higher level (Muller, 1970) and is of limited assistance in determining histories of lineages on the scale desirable in biogeographic analyses. Further, the upland Eocene megafossil assemblages from the northern Rocky Mountain region have been actively collected and studied for only the last two decades. These assemblages are critical because they contain the records of diversification of many microthermal groups (see below), and additional collecting and study are needed. In contrast, the Oligocene and Neogene

plant-megafossil assemblages from adjoining regions such as the Columbia Plateaus and from possible source areas such as Beringia are well known. Estimates based on the geographic and climatic distribution of fossil and extant taxa indicate that, at least in the Beringian Neogene, the lineages represented in the fossil record are thought to be more than 95% complete for woody plants.

Inferences also can be made regarding histories of lineages if a cladistic analysis of a group is combined with detailed knowledge of history of the physical environment. This approach, termed "vicariance biogeography" (e.g., Platnick & Nelson, 1978) has considerable merit for groups that have poor or no fossil records. However, it rests on major assumptions and requirements:

- (1) Cladistic analyses inherently rest on the assumption of parsimony in evolution of characters.
- (2) Cladistic analyses must be based on valid determination of polarities of character states.
- (3) History of the physical environments in all areas must be known in detail.
- (4) The final biogeographic analysis also rests on the assumption of parsimony in dispersals.

In most recent applications, vicariance biogeographers have either ignored the fossil record or, at best, have incorporated fossil taxa in cladistic analyses without reference to stratigraphy, although Grande (1985) emphasized the significance of the age relations of fossil taxa, which provide additional geographic data on distributions. Another major tendency has been to consider the history of the physical environment solely in terms of plate tectonics, thus ignoring particularly climatic changes. Because climates of a given area generally determine vegetational types and, in turn, vegetation organizes the environment into a variety of microenvironments (Upchurch & Wolfe, 1987) that determine whether a particular organism can live in a given area, the history of vegetation assumes paramount importance for interpreting the biogeographic histories of land organisms.

The fossil record can be of major significance in any analysis in vicariance biogeography, as Grande (1985) emphasized. However, partly because Grande was examining the fossil record from the standpoint of ichthyology, some contributions of paleontology to vicariance biogeography were not stressed or were overlooked:

- (1) The stratigraphic sequence of grades, if cautiously interpreted, can determine polarity states (Hennig, 1966).
- (2) The fossil record can supply evidence of environments in particular areas at particular times.
- (3) The fossil record can supply evidence of the existence of dispersal barriers and routes other than those related to plate tectonics.
- (4) The fossil record can supply minimal times of divergences in a cladogram, and these times can then be placed in the framework of the then-existing environments to determine probabilities of dispersals of the resulting, diverging lineages.
- (5) The fossil record can independently test the assumptions of parsimony in both evolution and dispersal.

Unfortunately, almost no cladistic analyses of groups of concern in the northern Rocky Mountains have been carried out. However, the results of a cladistic analysis of *Acer* (Wolfe & Tanai, 1987) when compared with the known fossil record of *Acer* (especially in North America) indicate:

- (1) The known relative times of appearances of sections of *Acer* generally correspond to those predicted from the cladogram; those few that do not correspond probably resulted from the absence of collections from the appropriate environment or areas.
- (2) Phylogeny reconstructed on a phenetic paleobotanical basis compares well with phylogeny reconstructed on a cladistic basis.
- (3) Dispersals have not been as parsimonious as would be predicted from vicariance biogeography.
- (4) The present distributions of species and sections of *Acer* are complex and have resulted from a variety of environmental, particularly climatic, factors.

As more cladistic analyses of extant groups are completed, they will provide a framework for evaluating phenetic paleobotanical phylogenies, but cladistic analyses, because of biogeographic "noise," can provide only highly generalized concepts of histories of biogeographic patterns, some of which are much more complex than indicated by cladistics alone and some of which are invalid (Wolfe, 1981b). In essence, cladistic analyses test phenetic phylogenies based on the fossil record, whereas the fossil record tests

models developed from vicariance biogeography.

The divergence that apparently exists between "vicariance" and "dispersalist" schools of biogeography has resulted from psychological and sociological factors. Each school typically has rejected the totality of the other's methods and results. Both have inherent problems that can be resolved by reference to the other's methods and/or by using the other's conclusions. Indeed, Grande's (1985) discussion of vicariance biogeography basically incorporates some dispersalist concepts and uses some dispersalist data that support his conclusions; he argued for systematic/biogeographic analyses on successive time planes to attempt to filter out biogeographic "noise" introduced by subsequent dispersal events. The approach used in the present report similarly will involve both cladistic and dispersalist concepts and data.

CRETACEOUS

The northern Rocky Mountain region was occupied by a mesothermal, broad-leaved evergreen forest during the Late Cretaceous (Dorf, 1942). Some conifers (e.g., Araucariaceae, evergreen Taxodiaceae) probably were emergents in this vegetation (Wolfe & Upchurch, 1987b), and broad-leaved deciduous plants were restricted largely to successional or disturbed vegetation, especially along streams. General absence of drip-tips and a somewhat small leaf size indicate slightly subhumid conditions (Wolfe & Upchurch, 1986, 1987a). Analyses of woods from the North American mesothermal region suggest little seasonality of either temperature or precipitation (Wolfe & Upchurch, 1987b). Presence of extensive marine rocks of Late Cretaceous age throughout much of the Western Interior indicates generally low altitudes.

Miller (1987) emphasized the great floristic disparity between known Early Cretaceous floras, including those of the northern Rocky Mountain region, and the modern flora of this region. Even with the rise to dominance of the angiosperms in the early Late Cretaceous, the flora has an archaic aspect, dominated by generalized members of Hamamelididae and Rosidae (Crabtree, 1987). Whether any of these ultimately gave rise to taxa that now occur in the northern Rocky Mountains cannot now be determined. By the later part of the Late Cretaceous, some families that today have microthermal members become recognizable. Aceraceae,

for example, occur in the latest Cretaceous of central Alberta, represented by an extinct genus interpreted as a sister group to *Acer* (Wolfe & Tanai, 1987). Even at high paleolatitudes, the flora was composed largely of trochodendroids, hamamelidaleans, and deciduous Taxodiaceae (Spicer et al., 1987); this high-latitude flora has some floristic similarities to that of the early Tertiary of the northern Rocky Mountains but no similarity to the extant flora of this region.

PALEOCENE

In areas such as eastern Montana, the Cretaceous–Tertiary boundary is marked by a presumed fallout layer that has anomalously high amounts of iridium and shocked minerals (Bohor et al., 1984); these are considered to be evidence of an impact by an extraterrestrial body (Alvarez et al., 1984). This event at the end of the Cretaceous had a profound effect on the flora and vegetation of the northern Rocky Mountain region (Wolfe & Upchurch, 1986). At least 50–60% of the latest Cretaceous lineages became extinct (Hickey, 1981). Most extinctions were in the previously dominant broad-leaved evergreen element; in addition, araucarians and many other evergreen conifers became extinct in this region. Immediately above the presumed fallout horizon, palynofloras contain almost exclusively fern spores (Hotton, 1984; Tschudy & Tschudy, 1986). Within a few centimeters above this horizon, angiosperm pollen occurs with the fern spores; the associated leaf flora contains both fern pinnae and a compound-leaved rosid, which is thin-leaved and probably deciduous. About 10 meters higher in the section, the leaf assemblage of about 15 species consists almost entirely of deciduous angiosperms (trochodendroids, hamamelidaleans, Tiliaceae) and deciduous conifers (Taxodiaceae).

The eastern Montana sequence immediately above the Cretaceous–Tertiary boundary resembles normal secondary succession following a volcanic eruption (Richards, 1952); in mesothermal, broad-leaved evergreen regions, deciduous plants are typically dominant in secondary successions (Wang, 1961). However, in the northern Rocky Mountain region, broad-leaved deciduous plants dominated north of the Colorado–Wyoming border (Brown, 1962), and the broad-leaved evergreen element did not return to dominance until almost the end of the Paleocene, about 10 Ma following the Cretaceous. Hickey (1981, 1984) attributed the deciduous-

ness of this Paleocene vegetation to an overall decline in temperature that persisted through most of the Paleocene. The occurrence of large (and presumably ectothermic) reptiles (crocodilians, champsosaurs, large turtles) with this deciduous vegetation, however, indicates the probable absence of low winter temperatures that would select for deciduousness. That is, the faunal data indicate strongly that the deciduousness of the vegetation is anomalous; just as significantly, megathermal, broad-leaved evergreen vegetation persisted in the early Paleocene at about the Colorado–Wyoming border.

Wolfe & Upchurch (1986) suggested instead that the terminal Cretaceous event resulted in a brief low-temperature excursion that devastated the vegetation of both mesothermal and megathermal regions of North America. Some megathermal, broad-leaved evergreen lineages survived (perhaps in refugia; Tschudy et al., 1984), and megathermal vegetation continued to be dominantly evergreen. The megathermal vegetation underwent physiognomic change and gradually increasing diversity during the Paleocene, a phenomenon mimicking short-term secondary succession and termed “quasisuccession” by Wolfe & Upchurch (1986, 1987a). However, almost none of the mesothermal, broad-leaved evergreen lineages survived, and replenishment of them would have had to occur by adaptation of some megathermal lineages to mesothermal climate on an evolutionary (not successional) time scale.

The anomalously deciduous character of Paleocene mesothermal vegetation throughout North America (and in Eurasia) gave deciduous angiosperms a unique opportunity. These deciduous lineages were derived primarily from elements that were uncommon in Late Cretaceous mesothermal evergreen vegetation and/or dominant in Late Cretaceous, high-latitude deciduous vegetation (Wolfe & Upchurch, 1986). In mesothermal regions, dominantly deciduous taxa (e.g., Hamamelidaceae, Fagaceae, Betulaceae, Ulmoideae, Juglandaceae) diversified during the Paleocene (e.g., Nichols & Ott, 1978; Manchester, 1987). By the end of the Paleocene, the Northern Hemisphere had a considerable diversity of broad-leaved deciduous plants, and many families of woody angiosperms that now occur in the Rocky Mountain region were extant.

A major increase in precipitation occurred at the Cretaceous–Tertiary boundary. In the northern Rocky Mountain region this is evidenced by

a substantial increase in leaf size and by the initiation of wide-scale peat deposition that typically marks the early Paleocene in this region (Wolfe & Upchurch, 1986). Not only would increased precipitation result in an increase in biomass, but water tables also would be raised and more swamps developed.

Pre-Eocene microthermal vegetation contrasts markedly with Eocene and later microthermal vegetation in floristic composition. Pre-Eocene microthermal vegetation was restricted to high latitudes and, probably due to low winter light levels, was almost entirely deciduous (Wolfe, 1985; Spicer & Parrish, 1986). The flora primarily comprised deciduous Taxodiaceae, deciduous Pinaceae (*Pseudolarix*), and deciduous dicotyledons, the great majority of which represents a few clades of trochodendrales, platanoids, and other hamamelidales (Spicer et al., 1987; Wolfe, 1987). Although these clades later contributed some lineages first to the mesothermal deciduous vegetation of the Paleocene and then to the Eocene upland microthermal vegetation, they comprise a small fraction of the Eocene and later microthermal flora. The microthermal vegetation and flora of the Late Cretaceous and the Paleocene have few similarities to Eocene and later vegetation and flora.

EOCENE

A warming initiated during the latest Paleocene culminated in the early Eocene thermal maximum (Savin, 1977; Wolfe & Poore, 1982; Wolfe, 1985). Vegetation in areas such as northwestern Wyoming was dominantly broad-leaved evergreen and represented warm mesothermal temperatures (Wing, 1981, 1987). At somewhat lower altitudes (and particularly in the lowland Pacific Northwest), vegetation represented megathermal rain forests (Wolfe, 1978, 1985). That the eastern part of the Rocky Mountain region was still generally of low altitudes is indicated by the persistence of large lakes from the early into late Eocene in areas such as southwestern Wyoming and adjacent Utah. The early Eocene vegetation indicates abundant precipitation, but later Eocene vegetation indicates increased seasonality of precipitation and development of subhumid, seasonal climate (MacGinitie, 1969; Leopold & MacGinitie, 1972).

The warm mesothermal to megathermal vegetation of the early and middle Eocene has few floristic similarities to the extant flora of the northern Rocky Mountains. A few extant north-

ern Rocky Mountain genera (e.g., *Alnus*, *Populus*, and *Acer*) are present in this vegetation, but the species represented are not closely related to extant species in this region.

Extensive volcanism and associated tectonism resulted in a major upland region that extended from northern Nevada and central Idaho north into British Columbia during the middle Eocene (Axelrod, 1966a, 1966b); this upland may have actually been a series of upland volcanic centers. Known upland assemblages of early middle Eocene age (Fig. 1) occur from northeastern Washington (Republic and associated floras) northward into central British Columbia (Princeton, Chu Chua Creek, and coeval floras). Extensive volcanism of early Eocene age became less intense during the early middle Eocene, and tectonism resulted in a series of grabens, in which the plant-bearing lacustrine sediments were deposited (Pearson & Obradovich, 1977). Altitude of the Republic basin of deposition is estimated to have been about 900 m (Wolfe & Wehr, 1987).

Later in the middle Eocene and in the early part of the late Eocene, major volcanic centers occurred in central Idaho (Challis Volcanics), central Oregon (Clarno Formation), and northeastern Nevada (rocks containing the Copper Basin and Bull Run floras of Axelrod, 1966b). Most Clarno assemblages represent only low altitudes, but a newly collected assemblage (Sheep Rock Creek) from the Crooked River Basin is probably microthermal and indicates the presence of higher altitudes. By the late Eocene, tectonism in the central Idaho region resulted in the formation of grabens and associated lakes on the post-Challis surface; these lake beds contain floras such as the Salmon. A similar depositional regime occurred in southwestern Montana (the numerous floras described by Becker); to the north in western Montana are plant-bearing lacustrine beds that have been collected recently by C. N. Miller and associates.

The development of this upland region, concomitant with a general decline of temperature following the early Eocene thermal maximum, resulted in the presence of microthermal climates. Early middle Eocene microthermal vegetation, such as that at Republic (Wolfe & Wehr, 1987), represents the oldest known coniferous forest dominated by Pinaceae (*Abies*, *Picea*, *Pinus*, *Pseudolarix*, and *Tsuga*) and Cupressaceae (*Chamaecyparis* and *Thuja*). These genera were of low diversity in the early middle Eocene, but had increased in diversity by the end of the

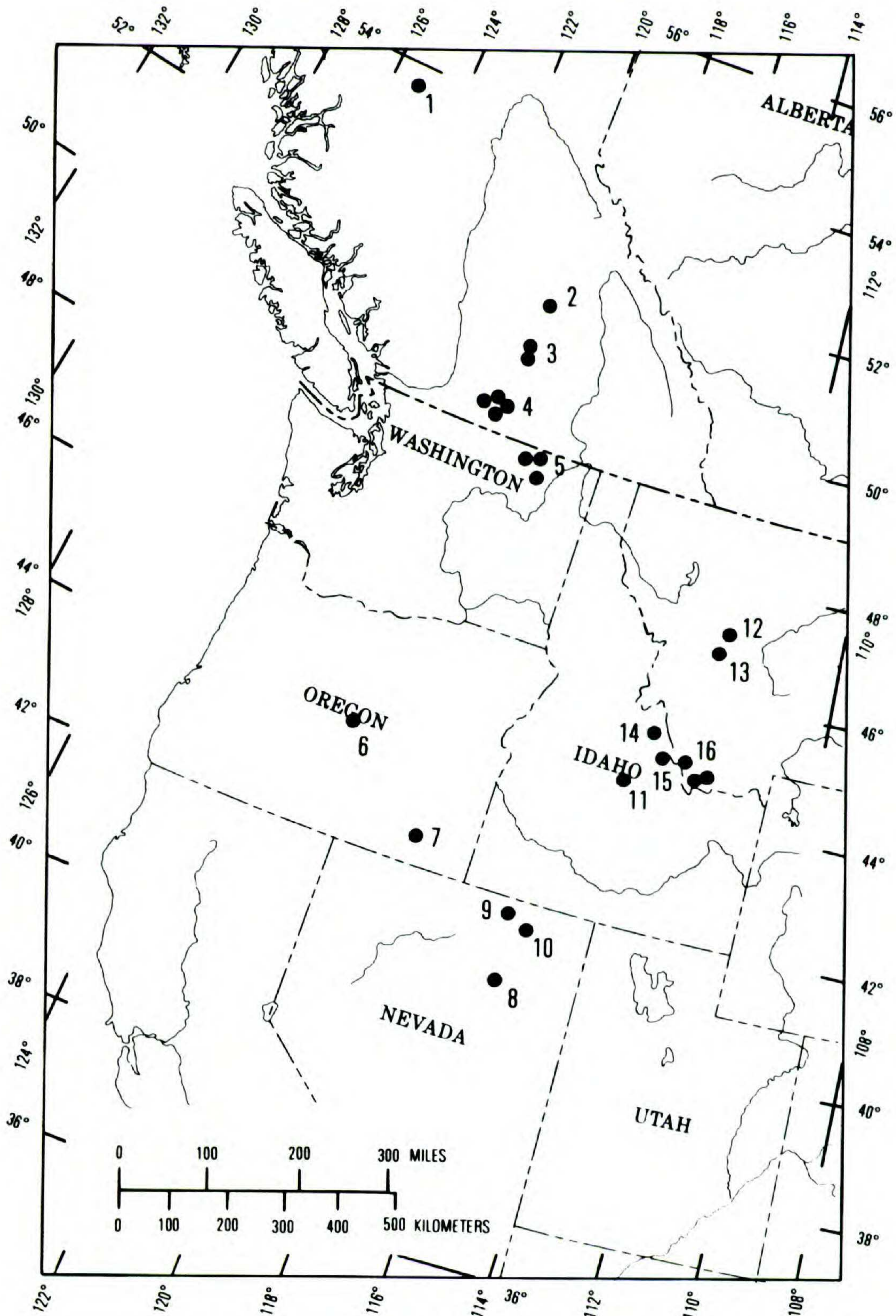


FIGURE 1. Map showing location of Eocene microthermal plant assemblages in western conterminous United States and adjacent Canada. For each assemblage or group of assemblages, either published references or repositories of largely unpublished assemblages are cited. These repositories are: GSC (Geological Survey of Canada); OMSI (Oregon Museum of Science and Industry); TMP (Tyrrell Museum of Paleontology); UAPC (University of Alberta Paleobotany Collections); UBC (University of British Columbia); UCMP (University of California Museum of Paleontology); UMPC (University of Montana Paleobotany Collections); USGS (U.S. Geological Survey); UWBM (University of Washington Burke Museum). Early middle Eocene: 1. Smithers (UWBM); 2. Chu Chua Creek (Berry, 1926); 3. Kamloops assemblages (TMP); 4. Princeton assemblages (GSC, UAPC, UWBM); 5. Republic assemblages (Wolfe & Wehr, 1987; UWBM). Late middle to early late Eocene: 6. Sheep Rock Creek (OMSI); 7. Alvord Creek (Axelrod, 1944b); 8. Elko assemblages (UCMP, USGS); 9. Bull Run assemblages (UCMP); 10. Copper Basin (Axelrod, 1966a); 11. Thunder Mountain (Brown, 1937). Latest Eocene: 12. Beaver Creek (UMPC); 13. Drummond (Pearson, 1972); 14. Salmon (Brown, 1937; USGS); 15. Cow Creek (USGS); 16. Beaverhead, Metzel Ranch, Mormon Creek, Ruby, and York Ranch (Becker, 1960, 1961, 1969, 1972, 1973).

Eocene. As discussed later, major diversification also occurred in numerous woody dicotyledonous families. This probably resulted from (1) the areal restriction of microthermal climate during the early Eocene and (2) the opportunistic expansion of mesothermal lineages into newly created microthermal climate in the uplands.

Areas of microthermal climate were probably highly restricted during the early Eocene thermal maximum. Indeed, I know of no latest Paleocene or early Eocene Northern Hemisphere plant assemblage that represents microthermal vegetation; possibly only on mountains in polar latitudes could such vegetation have been present (Wolfe, 1985, fig. 5). Because of the absence or extreme restriction of microthermal climates during the early Eocene, probably few pre-Eocene microthermal taxa were able to survive this climatic-geographic bottleneck, leaving the newly expanding microthermal regions available for opportunistic mesothermal lineages. Further, topographic and edaphic diversity, juxtaposition of many microclimates, and relative isolation of one volcanic center from another would all lead to rapid diversification of lineages in the uplands. Geographic proximity to lowland mesothermal vegetation would allow a continuing supply of new clades.

Probable instability of community composition during the middle Eocene is indicated by two lines of evidence. First, from one approximately coeval depositional site to another, species composition varies markedly; almost all the localities are in lacustrine shales and presumably represent similar ecologic settings. Spatial heterogeneity more resembled that of mesothermal or even megathermal vegetation than that of microthermal vegetation. Second, floristic comparisons of early middle Eocene lacustrine assemblages with late middle to early late Eocene assemblages indicate large changes in composition, some related to evolution of lineages within microthermal vegetation and some related to additions from mesothermal vegetation, as well as to extinction.

Numerous mesothermal (or mesothermal/megathermal) evergreen dicotyledonous clades had adapted to the microthermal climate by the early middle Eocene, although these typically are rare elements. Such taxa include *Talauma* (Magnoliaceae), *Phoebe* (Lauraceae), *Gordonia* (Theaceae), *Barghoornia* (Burseraceae), *Paullinia*, *Serjania*, and *Allophylus* (Sapindaceae), *Paleophytocrene* (Icacinaceae), and *Schoepfia* (Olaca-

ceae). None of these genera are known to have survived into microthermal vegetation of the late Eocene and they can best be considered as unsuccessful experiments, although other evergreen dicotyledons successfully adapted to the microthermal climate during the Eocene. The presence of evergreen dicotyledons in microthermal coniferous forests during the Eocene is consistent with the low (ca. 5°C) mean annual range of temperature inferred for coeval lowland assemblages (Wolfe, 1978). Modern microthermal coniferous vegetation of low-latitude, upland areas (e.g., Taiwan, Himalayas) also has many taxa of evergreen dicotyledons.

Also included in the upland early middle Eocene vegetation are numerous extant genera of trees and shrubs that contributed to broad-leaved deciduous and coniferous forests of the Neogene and Holocene, although not present in the northern Rocky Mountain region today. Included are: *Sassafras*, *Cercidiphyllum*, *Corylopsis*, *Comptonia*, *Castanea*, *Fagus*, *Tilia*, *Ulmus*, *Itea*, *Photinia*, *Decodon*, *Rhus*, and *Aesculus*.

Overall, diversity among woody angiosperms appears to have been higher in the initial phase (early middle Eocene) of development of the microthermal coniferous forests than later in the Eocene. At least 95 genera and 140 species of woody angiosperms are known in the Republic and Princeton floras, which are still not thoroughly collected. In contrast, about 70 genera and 110 species of woody angiosperms are known in the extensively collected and described latest Eocene coniferous forests from western Montana (Becker, 1960, 1961, 1969, 1972, 1973). This general decrease is particularly notable in presumed large trees, which were perhaps gradually replaced by newly evolved species of conifers.

Very few of the extant northern Rocky Mountain lineages are recognizable by the early middle Eocene. The oldest known *Betula* clearly allied to the *B. papyrifera*-*B. occidentalis* complex occurs at Republic, as does an *Acer* allied to *A. negundo*. However, the *Acer*, although possibly ancestral to *A. negundo*, is assignable to an extinct section (Wolfe & Tanai, 1987). Many other extant native microthermal genera were also participants in this early middle Eocene vegetation (e.g., *Alnus*, *Corylus*, *Ribes*, *Rubus*, *Spiraea*, *Crataegus*, *Prunus*, and *Cornus*), but the species cannot be placed directly in the ancestry of extant northern Rocky Mountain lineages.

The early middle Eocene microthermal flora

of western North America had numerous archaic elements in terms of Neogene or Holocene microthermal vegetation. Other than the unsuccessful thermophilic experiments previously listed, the vegetation had extinct genera of Trochodendraceae, Cercidiphyllaceae, Hamamelidaceae, Platanaceae, Fagaceae, Betulaceae, Rosaceae, and other families; about 40% of the genera are totally extinct (Wolfe & Wehr, 1987, unpubl. data).

By the late middle to late Eocene, upland microthermal vegetation had been floristically altered as the result of:

- (1) Extinction, e.g., the unsuccessful thermophilic experiments.
- (2) Gradual evolution in phylads, e.g., in a phylad ultimately leading to *Chamaebatiaria* (Rosaceae), the early middle and late Eocene members represent distinct genera.
- (3) Major diversification of early middle Eocene microthermal clades, e.g., whereas early middle Eocene *Acer* comprised 10 species and 3 extinct sections, late middle to late Eocene *Acer* comprised 35 species and 17 sections, 14 of which are extant (including the first members of sects. *Negundo* and *Macrophylla*).
- (4) Adaptation of members of previously mesothermal clades to microthermal climates, e.g., invasion of newly evolved species of *Quercus*, *Mahonia*, Salicaceae, and Leguminosae.

Rosaceae and Aceraceae underwent major diversification in Eocene upland microthermal vegetation. Both are today primarily bee-pollinated; entomophily would have been advantageous to small trees and shrubs in densely stocked coniferous forests. Diaspores of Rosaceae are typically biotically dispersed, as are those from some extant acers. Anemophily and abiotic dispersal, in contrast, probably characterized woody angiosperms that are abundantly represented in the fossil assemblages and that were presumably of fluvial habitats: trochodendroids, hamamelidaleans, *Fagopsis*, most Betulaceae, *Comptonia*, and Ulmoideae. However, the fluvial habitat and concomitant anemophily/abiotic dispersal syndrome did not lead to more than species-level diversification in most of these groups.

The great majority of extant genera of woody microthermal angiosperms had evolved by the end of the Eocene, yet diversification in some genera and perhaps families had yet to occur:

- (1) In *Salix*, all known Eocene species are referable to subg. *Salix*.
- (2) Ericaceae were of low generic and specific diversity in the Eocene; thus far only *Rhododendron* (subg. *Rhododendron*) has been found in the upland Eocene vegetation, although several small Eocene leaves that lack diagnostic characters have been referred to *Vaccinium*.
- (3) Only a few scattered Eocene palynological records of Caprifoliaceae s. str. are known, e.g., *Diervilla* in the latest Eocene of Alaska (E. B. Leopold, written comm., 1970). A few nondiagnostic, microphyllous leaves have been referred to *Symphoricarpos*.

OLIGOCENE AND NEOGENE

Wide-scale deposition of lacustrine sediments apparently ended in the northern Rocky Mountains by the end of the Eocene (ca. 33 Ma)⁴. This termination presumably resulted from considerable uplift, leading to downcutting and erosion. At approximately the same time, a worldwide major climatic deterioration occurred (Wolfe, 1978), resulting in development of microthermal, broad-leaved, deciduous forest at low altitudes of middle latitudes and broad-leaved deciduous and coniferous forests at high latitudes (Wolfe, 1985). This deterioration involved a decline in mean annual temperature and a major increase in mean annual range of temperature (Wolfe, 1978).

Megafloras of Oligocene and Neogene age are not known from the northern Rocky Mountains. Wing (1987) and Leopold & Denton (1987) have therefore largely concentrated on well-known assemblages from the adjacent Columbia Plateaus (Fig. 2). From the Oligocene into the middle Miocene (ca. 13–14 Ma), the Columbia Plateaus were occupied largely by Mixed Mesophytic forest; during the middle Miocene, this forest was replaced by Mixed Coniferous forest (Wolfe, 1981a).

That Miocene basalts of the Columbia River Group generally lap onto highlands to the east and north indicates that certainly the region of the northern Rocky Mountains was higher than

⁴ Many workers place the Eocene–Oligocene boundary at about 37 Ma and would include the latest Eocene floras discussed above in the early Oligocene. Whichever placement is valid does not affect relative or actual ages of the floras or paleoclimatic changes.

the Columbia Plateaus. Based on the temperature relations of extant vegetational types (Wolfe, 1979), I infer that during the Oligocene through middle Miocene, the northern Rocky Mountains had a lower altitudinal belt of Mixed Northern Hardwood forest (Fig. 3) and an upper belt of High Montane Mixed Coniferous forest (the vegetational type that generally occupies mesic sites within the present northern Rocky Mountains).

The terminal Eocene temperature deterioration resulted both in numerous microthermal lineages migrating downslope from Eocene uplands into Oligocene lowlands and in extinction of many microthermal lineages. For example, the relationships of most Bridge Creek (early Oligocene) taxa are with Eocene upland taxa (MacGinitie, 1953) and not with Eocene high-latitude taxa. Among the Oligocene taxa that illustrate this relationship are: *Cercidiphyllum crenatum*, *Castanea orientalis*, *Fagus pacifica*, *Quercus clarnensis*, *Alnus* "carpinoides," *Betula* aff. *papyrifera*, "Carpinus grandis," *Mahonia simplex*, *Plafkeria* sp., "Ulmus" *brownelli*, *Ame-lanchier* sp., *Crataegus newberryi*, *Acer* (*Negundo*) sp., *A. (Macrophylla) osmonti*, *A. (Lithocarpa)* sp., *Bohlenia* sp. (an extinct sapindaceous genus that = *Dipteronia* auct.), and "Holmskioldia" *speirii*. Some lowland Oligocene taxa were probably derived from mesothermal to megathermal taxa of the Eocene lowlands: *Liquidambar*, *Platanus*, *Engelhardtia*, and *Paleophytocrene*. Although such taxa are few, both *Liquidambar* and *Platanus* were vegetationally important during the Neogene. None of the Bridge Creek lineages appear to be derived from a northern source.

Although the Oligocene data base is not as complete as desired, many Eocene microthermal lineages are unknown in the Oligocene. Taxa that apparently became extinct at the end of the Eocene include *Fagopsis*, some genera of Rosaceae, and the sister genus of *Acer* ("Acer" *arcticum* group). Some Eocene microthermal lineages that participated in Oligocene vegetation of the Columbia Plateaus did not survive into the Miocene (e.g., "Zelkova," *Plafkeria*, *Bohlenia*, "Holmskioldia"). Clearly, extinction continued to play a significant role.

The Oligocene vegetation in high-latitude regions such as Alaska was of low diversity (Wolfe, 1972, 1985) and provided a limited reservoir for mid-latitude lineages. Only near the end of the Oligocene did taxonomic diversity increase in

high-latitude regions, largely from migration from lower latitudes and some diversification of immigrant clades; the influence at mid latitudes of the high-latitude flora was generally not felt until the middle and late Miocene.

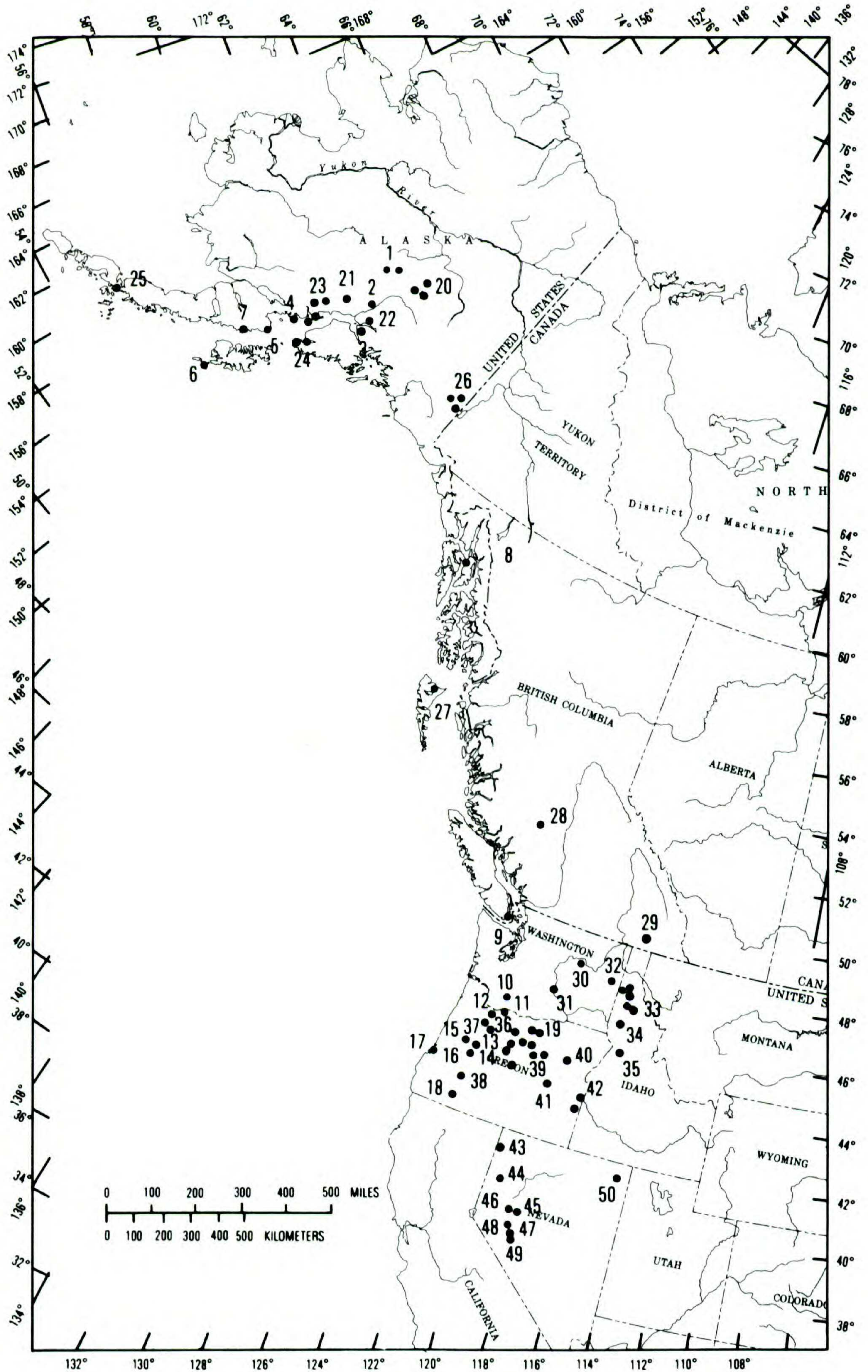
By the early to middle Miocene, the flora of the Columbia Plateaus had increased in diversity relative to the Oligocene. This diversity increase resulted from three major factors (Wolfe, 1972, 1977):

- (1) Adaptation of mesothermal lineages to microthermal climates (e.g., *Magnolia*, some Lauraceae, and *Exbucklandia*).
- (2) Diversification of Oligocene microthermal clades (e.g., *Fagus*, *Alnus*, *Ulmus*, *Carya*, and *Acer*).
- (3) Northward migration of Asian mid-latitude lineages into Beringia and subsequent southward migration onto the Columbia Plateaus (e.g., four lineages of *Acer* belonging to sections *Macrantha*, *Platanoidea*, and *Parviflora*).

Maximal diversity on the Columbia Plateaus and adjacent areas was reached during the middle Miocene (ca. 13–16 Ma).

Notable are the few species shared between middle Miocene floras on the Columbia Plateaus and the Kilgore flora of Nebraska (MacGinitie, 1962). Even a putative shared species (*Acer* "heterodontatum," in sect. *Negundo*) is represented in either region by distinct subspecies. Further, most Columbia Plateaus species have only a distant relationship to extant species of eastern North America. Divergences between most western and eastern American lineages had probably occurred during, or at the end of, the Eocene, which led to a distinctive western American element (Wolfe & Tanai, 1980: 16–18). By the Miocene (if not the Oligocene), the Rocky Mountain region must have formed an effective climatic barrier to migrations of most warm microthermal plants (Leopold & Denton, 1987).

An exception is series *Saccharodendron* of *Acer*, which was apparently able to disperse from eastern into western North America. Members of this series appear suddenly at middle latitudes of western North America during the early Miocene and have no Beringian record. Cladistic relationships and the fossil record both suggest dispersal across the North Atlantic during the Miocene (Wolfe, 1981b; Wolfe & Tanai, 1987), and the two lineages of series *Saccharodendron* present in the western American Neogene are



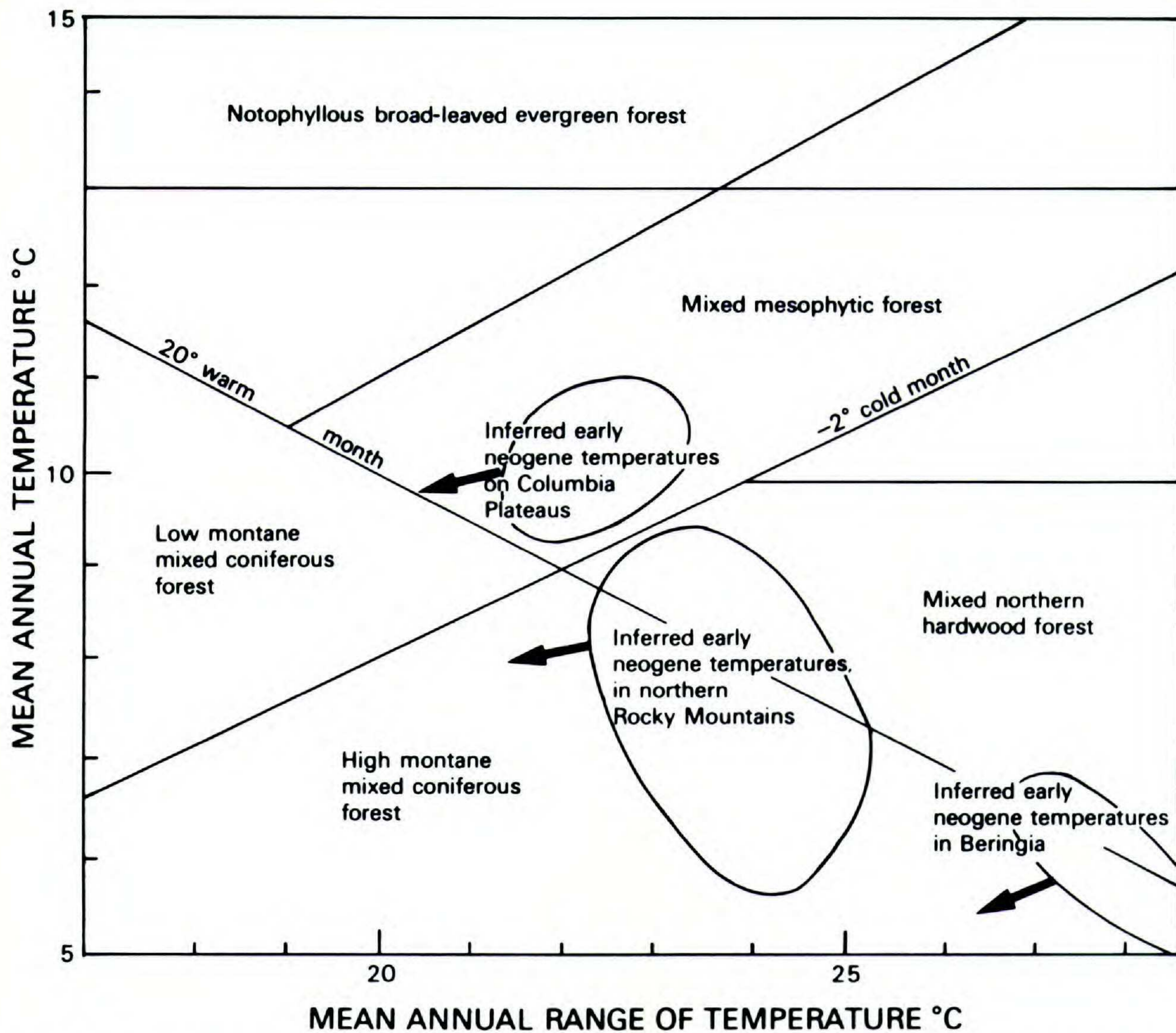


FIGURE 3. Nomogram showing inferred temperatures for the northern Rocky Mountains during the early Neogene. Classification and temperature relations of forests adapted from Wolfe (1979). Inferred temperatures for Columbia Plateaus and Beringian assemblages adapted from Wolfe & Tanai (1980) and Wolfe (1981a). Arrows indicate direction of Neogene temperature trends.

←

FIGURE 2. Map showing location of some Oligocene and early Neogene (>13 Ma) plant assemblages in western North America. For each assemblage or group of assemblages, either published references or repositories of largely unpublished assemblages are cited; see Figure 1 for explanation of repositories. Oligocene: 1. Cheenetchuk River assemblages (USGS); 2. Colorado Creek (USGS); 3. Eagle River (Wolfe et al., 1966); 4. Harriet Point, Harriet Creek, and Redoubt Point (USGS); 5. Douglas Mountain (USGS); 6. Sitkinak Island (USGS); 7. Kukak Bay assemblages (Knowlton, 1904; USGS); 8. Kootznahoo assemblages (Wolfe in Lathram et al., 1965); 9. Sooke (LaMotte, 1935; GSC); 10. Gumboot Mountain (UCMP); 11. Cascade Locks (USGS); 12. Sandstone Creek (USGS); 13. Cascadia (UCMP); 14. Lyons (Meyer, 1973); 15. Willamette (UCMP); 16. Rujada (Lakhanpal, 1958); 17. Yaquina (McClammer, 1978); 18. Shale City (USGS); 19. Bridge Creek assemblages (Chaney, 1927; OMSI, UCMP USGS). Early Neogene: 20. Nenana coal field assemblages (Wahrhaftig et al., 1969); 21. Lower Cache Creek (Wolfe et al., 1966); 22. Houston (Wolfe et al., 1966); 23. Capps Glacier (Wolfe, 1966; USGS); 24. Seldovia Point assemblages (Wolfe & Tanai, 1980); 25. Coal Bay (USGS); 26. Frederika (Wolfe, 1972; USGS); 27. Skonun (UBC); 28. Hanceville (GSC); 29. St. Eugene (Hollick, 1927); 30. Grand Coulee (Berry, 1931); 31. Vantage (UCMP); 32. Latah assemblages (Knowlton, 1926; Berry, 1929; Brown, 1937); 33. Clarkia (Smiley et al., 1975); 34. Orofino Creek (Brown, 1940); 35. Whitebird (Berry, 1934); 36. Eagle Creek assemblages (Chaney, 1920); 37. Collawash and Fish Creek (USGS); 38. Little Butte Creek (USGS); 39. Mascall assemblages (Chaney & Axelrod, 1959); 40. Baker (USGS); 41. Skull Spring (USGS); 42. Succor Creek assemblages (Graham, 1964, in part; cf. Fields, 1983); 43. '49 Camp (LaMotte, 1936); 44. Rabbit Hole (USGS); 45. Eastgate (Axelrod, 1985); 46. Middlegate (Axelrod, 1985); 47. Goldyke (UCMP); 48. Fingerrock (Wolfe, 1964); 49. San Antonio (UCMP); 50. Thurston Ranch (UCMP).

inferred to have crossed the Rocky Mountains; consistent with such crossings are the present distributions of the related *A. brachypterum* and the descendant *A. grandidentatum*, both of which live in the Rocky Mountains today. Thus some probably very limited floristic interchange between eastern and western North America occurred during the Neogene.

In the absence of actual assemblages, the flora of the northern Rocky Mountain region during the post-Eocene can be inferred only from assemblages outside the region. Except for floras to the west and southwest on the Columbia Plateaus, however, floras from adjacent regions are few. To the north in central British Columbia, the probable early Miocene assemblage from near Hanceville on the Chilcotin River appears to represent a High Montane Mixed Coniferous forest. In southern Colorado, the late Oligocene Creede assemblage represents subalpine coniferous vegetation. In Nebraska, the middle Miocene Kilgore assemblages largely represent a mesothermal gallery forest (MacGinitie, 1962).

Taxa that occurred both in Mixed Northern Hardwood forest of Alaska and in Mixed Mesophytic forest of the Columbia Plateaus represent taxa that (1) could exist under temperatures inferred for the northern Rocky Mountain region and (2) are known to have occurred adjacent to the northern Rocky Mountains. Such taxa thus can be reasonably inferred to have been in the northern Rocky Mountain region. Included in this category are lineages that are extant in the northern Rocky Mountains: *Alnus* aff. *incana*, *A.* aff. *viridis*, *Betula* aff. *papyrifera*, *Populus* aff. *trichocarpa*, *Salix* aff. *lasiandra*, *Prunus* aff. *virginiana*, *Acer* aff. *negundo*, and *A.* aff. *macrophyllum*. Also included are species of now extinct lineages: *Nordenskioldia* ("Cocculus" *auriculata*), *Cercidiphyllum alaskanum*, *Liquidambar pachyphylla*, *Alnus fairii*, *A. healeyensis*, *Ostrya oregoniana*, *Populus kenaiana*, *Ulmus knowltonii*, *U. speciosa*, *U. owyheensis*, *Zelkova brownii*, *Carya bendirei*, *Pterocarya nigella*, *Acer scottiae*, *A. septilobatum*, *A. tigilense*, and *Nyssa knowltonii*. Both lists contain primarily arcto-tertiary genera, genera that are now disjunct between eastern Asia and eastern North America or genera that are now characteristic of forests of north temperate regions (Engler, 1879). These genera (and many subgeneric groups), however, were represented in the Eocene upland microthermal vegetation; their inferred presence in the northern Rocky Mountain region is not necessarily the

result of southward migration from high latitudes.

Composition of the northern Rocky Mountain coniferous element during the Oligocene and Miocene must also be inferred. In the middle Miocene of Nevada, the conifers are primarily those that now inhabit Low Montane Mixed Coniferous forest (e.g., *Abies* aff. *concolor*, *Picea* aff. *breweriana*, *Pinus* aff. *monticola*, *P.* aff. *ponderosa*, *Tsuga* aff. *heterophylla*, and *Chamaecyparis* aff. *nootkatensis*). Most of these conifers were also dominants of the Columbia Plateaus vegetation between 10 and 13 Ma (Fig. 4). In at least one instance, the fossil species is a sister species to the lineage that gave rise to the extant species (Edwards, 1983), suggesting that the fossil may have been adapted to a different environment than the extant species.

In the Beringian Neogene, most coniferous lineages were distinct from mid-latitude lineages. The *Abies* belong to a group of which the extant *A. sibirica* and *A. grandis* are members. *Larix* was a diverse and major element in the Beringian Neogene; no valid *Larix* is known during the Miocene at middle latitudes of western North America (H. E. Schorn, pers. comm., 1984). The Beringian *Picea* either are related to extant Asian species or represent the *P. glauca* group (including an extinct, large-coned species that survived into the Wisconsin glacial of southeastern North America according to Critchfield, 1984). Thus, the conifers (*Abies grandis*, *Larix*, and *Picea glauca*) that are now the most distinctive element of the northern Rocky Mountain region relative to other regions of the western United States appear to be derived from a high-latitude source.

Precisely when the Beringian coniferous element arrived in the northern Rocky Mountains is unknown. I suggest, however, that the arrival was probably post-Miocene. Coniferous lineages allied to taxa that are now restricted to Low Montane Mixed Coniferous forest occupied the Columbia Plateaus and Nevada during the Neogene and presumably represent ecotypes distinct from extant relatives (Wolfe, 1964); such extinct ecotypes also may have occupied the northern Rocky Mountains during the Neogene. During the late Neogene, many of these northern Rocky Mountain conifers possibly became extinct as the Beringian lineages migrated south. Perhaps significant is that the first record of the coastal ecotype of *Abies grandis* at middle latitudes is in the Pliocene–Pleistocene Sonoma assemblage of California (Axelrod, 1944a).

Various dicotyledons also may have penetrated southward from high latitudes during the Neogene. All North American (including Beringian) Eocene *Salix* represent subg. *Salix*. In Beringia, subg. *Vetrix* appears in the late Oligocene, approximately coincidental with the first appearance of other taxa of Asian affinities; members of sect. *Glauceae* appear in Beringia by the early Miocene. Sect. *Retusae* of subg. *Chamaetia* appear by the end of the Miocene. Skvortsov (1968) suggested that subg. *Vetrix* and subg. *Chamaetia* were of Asian origin, based on the present distribution of species that have inferred primitive morphologies. Although Asian fossil data are lacking, certainly the Beringian data are consistent with Skvortsov's interpretations. During the Neogene, various members of subg. *Vetrix* and sect. *Glauceae* underwent diversification at high latitudes. A few lineages penetrated southward in North America by the late early Miocene and middle Miocene, but most lineages of subg. *Vetrix* and subg. *Chamaetia* now extant at middle latitudes of western North America are probably late Neogene immigrants.

Representatives of Caprifoliaceae such as *Diervilla*, *Lonicera*, and *Symphoricarpos* were also significant and diverse elements in the Beringian Miocene, as were Ericaceae such as *Rhododendron* (subg. *Anthodendron* = *Azalea*) and *Vaccinium*. These are generally absent in Neogene floras at middle latitudes, although *Symphoricarpos* is known in the late middle Miocene of Nevada (Axelrod, 1956) and the late Miocene of Idaho (Chaney & Axelrod, 1959). Presumably most Caprifoliaceae and Ericaceae also represent late Neogene immigrants into the northern Rocky Mountain region.

Some extant northern Rocky Mountain Rosaceae (e.g., *Amelanchier*) appear to be derived from lineages that have lived in or near the northern Rocky Mountain region since the Eocene. Other Rosaceae, however, probably belong to the late Neogene Beringian element. Although *Rubus* was represented in the Eocene upland microthermal vegetation, the extant *R. idaeus* has a probable ancestor in the Beringian Miocene. Similarly, *Prunus* subg. *Padus* has a continuous record in western North America during the Eocene and later, but subg. *Prunophora* first appears in western North America in Beringia during the Miocene, and the extant Pacific Northwest *Prunus subcordata* appears to represent a late Neogene immigrant from Beringia.

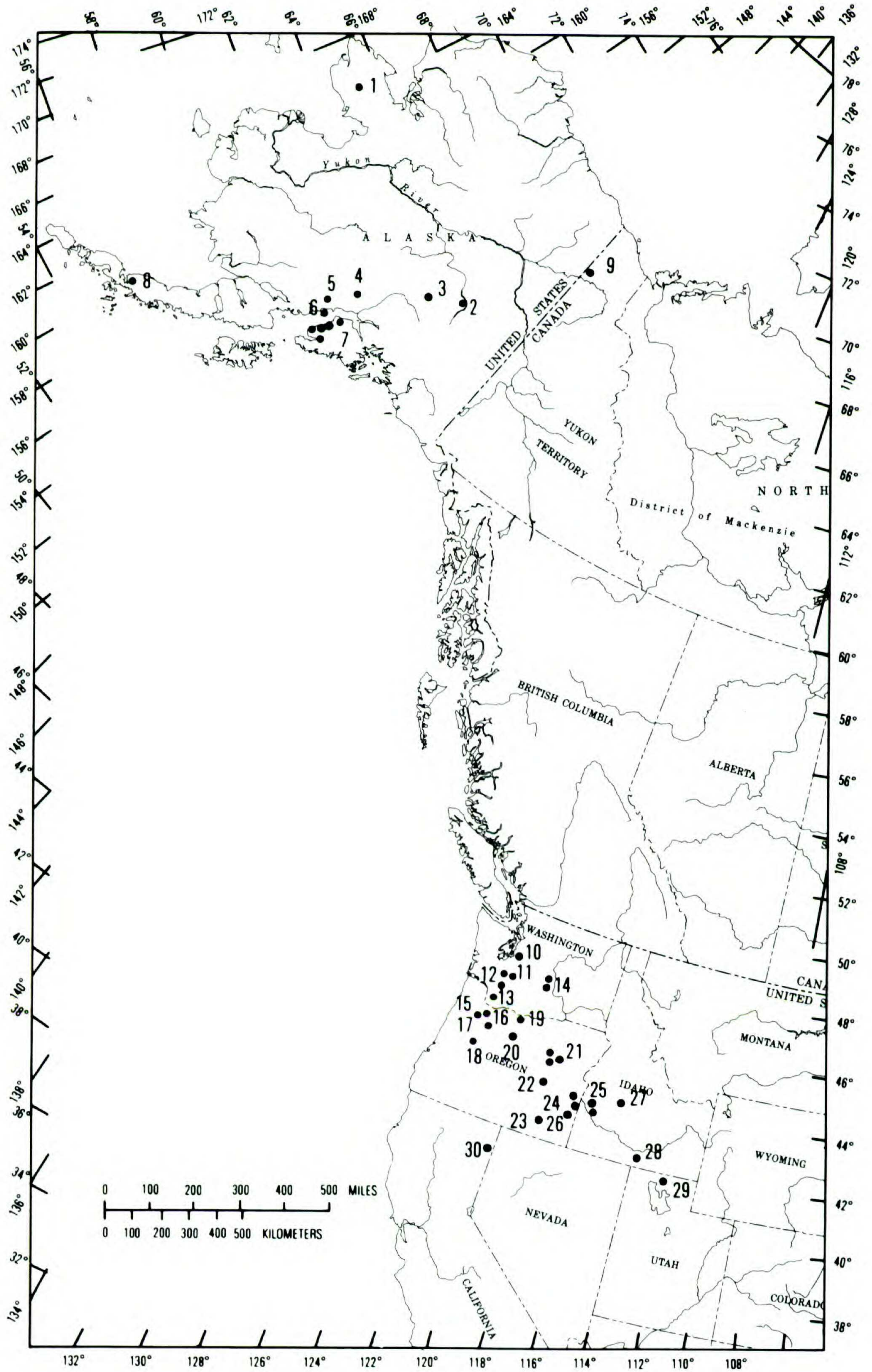
A pattern somewhat similar to that of *Prunus*

is indicated for *Alnus*. Members of subg. *Alnus* were present in the northern Rocky Mountain region as early as late Paleocene, and all the upland Eocene *Alnus* represent this subgenus. The mid-latitude members of the subgenus differentiated by the Oligocene into a lineage leading to the extant *A. oregona*, and the lineage is clearly recognizable in the early Miocene of Oregon. High-latitude members of the subgenus are recognizable as belonging to the *A. crispa* lineage by the Oligocene, and this lineage had penetrated into middle latitudes by the middle Miocene. Members of subg. *Alnobetula* are high-latitude in distribution through the Miocene, and the entry of the extant *A. viridis* into middle latitudes probably occurred during the late Neogene.

DISCUSSION

The terminal Cretaceous event selected for deciduousness and created a mesothermal region in the Northern Hemisphere almost devoid of broad-leaved evergreens, allowing by default occupation of this region by many deciduous groups. These groups then underwent major generic-level diversification. The elimination (or nearly so) of microthermal climates by the early Eocene thermal maximum and the following creation of microthermal, mid-latitude uplands of the later Eocene provided the opportunity for adaptive radiation of these deciduous mesothermal clades into the new microthermal environments and the opportunity for continuing diversification. Fundamentally, microthermal ecosystems became extinct during the early Eocene thermal maximum and arose again *de novo* following the thermal maximum. The continuing and major alterations in floristic composition during the Eocene, the apparent high degree of community instability during at least the early middle Eocene, and the rapid diversification of groups such as Rosaceae and Aceraceae during the Eocene can be viewed as symptomatic of the evolution of this new ecosystem. Insofar as known, the western North American volcanic uplands made up the only major, mid-latitude upland region in the Northern Hemisphere during the Eocene. These volcanic uplands thus occupy a central place in the diversification of many (if not most) microthermal clades of arcto-tertiary type.

Primarily during the middle and late Eocene, many microthermal, arcto-tertiary lineages were able to disperse readily from North America into Eurasia as adjuncts of a continuous expanse of coniferous forests (Wolfe, 1985, fig. 10). Partic-



ularly with the general cooling that characterized the later Eocene (Savin, 1977), microthermal climates were found at increasingly lower latitudes and produced a greater area available for occupation by microthermal vegetation. As migrating lineages elaborated over this area, diversification would continue and some new divergences that occurred in other regions would probably, in turn, migrate into North America. Thus, even in the Eocene, complexities were probably introduced into historical patterns of a given lineage.

Histories of the component lineages now in the flora of the northern Rocky Mountains are varied.

- (1) Some lineages can be traced back, more or less continuously, into microthermal vegetation of the Eocene uplands (e.g., *Betula papyrifera* complex).
- (2) Some lineages have generic representation in this upland vegetation, but divergences that led to the extant species probably occurred in the Oligocene or Neogene at middle latitudes (e.g., *Alnus oregona*) and some at high latitudes (e.g., *A. viridis*).
- (3) Some lineages represented in the Eocene uplands probably dispersed into Asia, underwent major divergences into new subgenera, returned to Beringia by the Neogene, underwent species-level diversification, and entered the northern Rocky Mountain region in the late Neogene (e.g., species of *Salix* subg. *Vetrix*).
- (4) Some lineages represented in the Eocene uplands dispersed into Eurasia, underwent diversification at the sectional level and returned to North America via long-distance dispersal from Europe (e.g., *Acer* series *Saccharodendron*).

- (5) Some lineages have long Beringian histories and entered the northern Rocky Mountain region during the late Neogene (e.g., *Lonicera*).
- (6) Another major pattern must be inferred for many alpine tundra plants; Arctic tundra is not recognizable until about the Pliocene–Pleistocene boundary (Wolfe, 1985), and elements shared between Arctic tundra and alpine tundra of the northern Rocky Mountain region may have entered the northern Rocky Mountains during the Quaternary.
- (7) Another pattern must be inferred for plants of subhumid to xeric, southern affinities (Barnosky, 1984; Leopold & Denton, 1987); some of these belong to families that did not originate until about 25 Ma (Muller, 1981). The Neogene spread of Compositae was rapid, probably in relation to the high degree of dispersibility of their diaspores; however, the spread appears to be associated also with the development of dry climates.
- (8) Pollen indicates that *Sarcobatus* (Chenopodiaceae) was a member of mesic coniferous forest during the later Miocene in areas such as southern Idaho (Wolfe, 1969); adaptation of *Sarcobatus* to xeric climate may be a late Neogene phenomenon.

No single pattern explains the origin of the majority of the modern flora of the northern Rocky Mountain region or even the majority of the flora of a given vegetational type or zone in the region. Certainly late Neogene cooling (probably along with orogenic movements) created climates in the northern Rocky Mountains favorable to Beringian taxa, but these are intermixed with taxa whose ancestry goes back to the Eocene in the northern Rocky Mountains. Further, Be-

←

FIGURE 4. Map showing location of some late Neogene (<13 Ma) plant assemblages in western North America. For each assemblage or group of assemblages, either published references or repositories of largely unpublished assemblages are cited; see Figure 1 for explanation of repositories. 1. Hoogendoorn (Hopkins et al., 1971); 2. McCallum Creek (USGS); 3. Grubstake (Wahrhaftig et al., 1969); 4. Upper Cache Creek (Wolfe et al., 1966); 5. Chuitna River (Wolfe, 1966); 6. Tyonek (Wolfe et al., 1966); 7. Assemblages of type and referred sections of Homerian and Clamgulchian Stages (Wolfe et al., 1966; Wolfe, 1966); 8. Herendeen Bay (USGS); 9. Porcupine River (UAPC); 10. Hammer Bluff (USGS); 11. Mashel assemblages (USGS); 12. Wilkes assemblages (USGS); 13. Woodland (UWBM); 14. Ellensburg assemblages (Smiley, 1963); 15. Troutdale (Chaney, 1944b); 16. Faraday (USGS); 17. Weyerhauser and Molalla (UCMP, USGS); 18. Hidden Lake (USGS); 19. The Dalles (Chaney, 1944a); 20. Deschutes (Chaney, 1938); 21. Austin, Tipton and Vinegar Creek (Chaney, 1959; Chaney & Axelrod, 1959); 22. Stinking Water (Chaney & Axelrod, 1959); 23. Trout Creek (MacGinitie, 1933; Graham, 1964); 24. Succor Creek assemblages (Graham, 1964, in part; cf. Fields, 1983); 25. Hog Creek (Dorf, 1936); 26. Payette assemblages (UCMP; cf. Fields, 1983); 27. Thorn Creek (Smith, 1941); 28. Trapper Creek (Axelrod, 1964); 29. Cache Valley (Brown, 1949); 30. Pit River (LaMotte, 1936).

ringian taxa entered at different times during the Neogene and even Quaternary.

Despite considerable resemblance at the generic level to the modern flora of the northern Rocky Mountains, the microthermal upland vegetation of the Eocene had many genera that are now extinct and many genera that are now exotic to the region. Microthermal vegetation of western North America experienced major floristic alteration during the Eocene and later in response to various extrinsic climatic factors and intrinsic biotic factors such as competition.

The primary floristic result of the terminal Eocene temperature deterioration for microthermal vegetation was the elimination of many dicotyledonous genera, particularly those containing evergreens. Many deciduous dicotyledons, however, also suffered extinction. For example, numerous lineages in *Acer* became extinct, including all North American members of sections *Acer*, *Platanoidea*, *Campestris*, and *Macrantha* (all of which survived in Eurasia). Patterns of survival among deciduous taxa differed markedly between Eurasia and North America, probably due to intrinsic factors.

The relatively depauperate flora of the early Oligocene offered opportunities for radiation and diversification, with a general increase in diversity and blurring of the regional Oligocene generic and subgeneric endemism, especially between western North America and eastern Asia; for example, both *Platanoidea* and *Macrantha* reappeared in western North America during the Neogene. Migrations across Beringia were enhanced by the mid-Miocene warm interval, when broad-leaved deciduous forests were probably continuous from the Pacific Northwest across Beringia and into middle latitudes of eastern Asia (Wolfe, 1985, fig. 11).

Cooling at about 13 Ma (late middle Miocene), concomitant with a general Neogene decline in summer temperatures and decline in mean annual ranges of temperature (Wolfe, 1981a), eliminated many broad-leaved taxa of trees and shrubs from the Columbia Plateaus, Beringia, and presumably the northern Rocky Mountains. Coniferous forests probably occupied a continuous belt from the Columbia Plateaus and the northern Rocky Mountains north into Beringia. Mixed Northern Hardwood forest would have been totally eliminated from western North America. Climates in the northern Rocky Mountain region during the Neogene may have initially exhibited the trend toward lower mean annual ranges of

temperature. However, by the late Miocene, increase in altitudes of mountains along the Pacific Coast would have countered this trend, allowing incursions of Arctic air masses; these masses are inferred to have influenced eastern North America after 13 Ma (Wolfe, 1985).

During the Neogene a summer-dry precipitation regime gradually encroached from the south (Wolfe, 1978), and during the late Miocene (ca. 5–11 Ma) increase in altitude of the Cascade Range created a significant rain shadow east of the range (Chaney, 1944c; Smiley, 1963). At lower altitudes on the Columbia Plateaus, forests were replaced by steppe vegetation during the late Miocene (Leopold & Denton, 1987; Wolfe, 1985). An analogous replacement was occurring in the northern Rocky Mountain region (Baranosky, 1984).

Considering the complexities of climatic changes and the complexities of orogenic activity in the northern Rocky Mountain and nearby regions, determination of historical biogeographic patterns, without recourse to the fossil record of extant lineages and analyses of successive fossil biotas, can be highly problematic. As Grande (1985) emphasized, vicariance methodology as typically applied is incapable of dealing with such complexities; several patterns can be overprinted on one another in such a region. Numerous patterns have been detected in the modern flora of the northern Rocky Mountains by recourse to the fossil record, and different species within the same genus can represent different patterns. Lineages, some closely related, can be subjected to the same extrinsic environmental factors and can respond in different ways, a fact that further increases the general complexity of the biogeographic tapestry in a region such as the northern Rocky Mountains.

LITERATURE CITED

- ALVAREZ, W., L. W. ALVAREZ, F. ASARO & H. V. MICHEL. 1984. The end of the Cretaceous: sharp boundary or gradual transition? *Science* 223: 1183–1186.
- AXELROD, D. I. 1944a. The Sonoma flora. Pp. 167–206 in R. W. Chaney (editor), *Pliocene Floras of California and Oregon*. Publ. Carnegie Inst. Wash. 553.
- . 1944b. The Alvord Creek flora. Pp. 225–262 in R. W. Chaney (editor), *Pliocene Floras of California and Oregon*. Publ. Carnegie Inst. Wash. 553.
- . 1956. Mio-Pliocene floras from west-central Nevada. *Univ. Calif. Publ. Geol. Sci.* 33: 1–322.
- . 1964. The Miocene Trapper Creek flora of

- southern Idaho. Univ. Calif. Publ. Geol. Sci. 51: 1-181.
- . 1966a. The Eocene Copper Basin flora of northeastern Nevada. Univ. Calif. Publ. Geol. Sci. 59: 1-125.
- . 1966b. A method for determining the altitudes of Tertiary floras. *Palaeobotanist* 14: 144-171.
- . 1985. Miocene floras from the Middlegate Basin, west-central Nevada. Univ. Calif. Publ. Geol. Sci. 129: 1-279.
- BARNOSKY, C. W. 1984. Late Miocene vegetational and climatic variations inferred from a pollen record in northwest Wyoming. *Science* 223: 49-51.
- BECKER, H. F. 1960. The Tertiary Mormon Creek flora from the upper Ruby River Basin in southwestern Montana. *Palaeontographica, Abt. B, Paläophytol.* 107: 83-126.
- . 1961. Oligocene plants from the upper Ruby River Basin, southwestern Montana. *Mem. Geol. Soc. Amer.* 82: 1-127.
- . 1969. Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana. *Palaeontographica, Abt. B, Paläophytol.* 127: 1-142.
- . 1972. The Metzel Ranch flora of the upper Ruby River Basin, southwestern Montana. *Palaeontographica, Abt. B, Paläophytol.* 141: 1-61.
- . 1973. The York Ranch flora of the upper Ruby River Basin, southwestern Montana. *Palaeontographica, Abt. B, Paläophytol.* 143: 18-93.
- BERRY, E. W. 1926. Tertiary floras from British Columbia. *Bull. Geol. Surv. Canada* 42: 91-116.
- . 1929. A revision of the flora of the Latah Formation. *U.S. Geol. Surv. Prof. Pap.* 154-H: 225-265.
- . 1931. A Miocene flora from Grand Coulee, Washington. *U.S. Geol. Surv. Prof. Pap.* 170-C: 31-42.
- . 1934. Miocene plants from Idaho. *U.S. Geol. Surv. Prof. Pap.* 185-E: 97-125.
- BOHOR, B. F., E. E. FOORD, P. J. MODRESKI & D. M. TRIPLEHORN. 1984. Mineralogic evidence for an impact event at the Cretaceous-Tertiary boundary. *Science* 224: 867-869.
- BROWN, R. W. 1937. Additions to some fossil floras of the western United States. *U.S. Geol. Surv. Prof. Pap.* 186-J: 163-206.
- . 1940. New species and changes of name in some American fossil floras. *J. Wash. Acad. Sci.* 30: 344-356.
- . 1949. Pliocene plants from the Cache Valley, Utah. *J. Wash. Acad. Sci.* 39: 224-229.
- . 1962. Paleocene flora of the Rocky Mountains and Great Plains. *U.S. Geol. Surv. Prof. Pap.* 375: 1-119.
- CHANEY, R. W. 1920. The flora of the Eagle Creek Formation. *Contr. Walker Mus.* 2: 115-181.
- . 1927. Geology and paleontology of the Crooked River Basin with special reference to the Bridge Creek flora. *Publ. Carnegie Inst. Wash.* 346: 45-138.
- . 1938. The Deschutes flora of eastern Oregon. *Publ. Carnegie Inst. Wash.* 476: 187-216.
- . 1944a. The Dalles flora. *In* R. W. Chaney (editor), *Pliocene Floras of California and Oregon*. *Publ. Carnegie Inst. Wash.* 553: 285-321.
- . 1944b. The Troutdale flora. *In* R. W. Chaney (editor), *Pliocene Floras of California and Oregon*. *Publ. Carnegie Inst. Wash.* 553: 323-351.
- . 1944c. Summary and conclusions. *In* R. W. Chaney (editor), *Pliocene Floras of California and Oregon*. *Publ. Carnegie Inst. Wash.* 553: 353-383.
- . 1959. Miocene floras of the Columbia Plateau, composition and interpretation. *Publ. Carnegie Inst. Wash.* 617: 1-134.
- & D. I. AXELROD. 1959. Miocene floras of the Columbia Plateau, systematic considerations. *Publ. Carnegie Inst. Wash.* 617: 135-237.
- CRABTREE, D. R. 1987 [1988]. Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. *Ann. Missouri Bot. Gard.* 74: 707-747.
- CRITCHFIELD, W. B. 1984. Impact of the Pleistocene on the genetic structure of North American conifers. Pp. 70-118 *in* R. M. Lanner (editor), *Proceedings of the Eighth North American Forest Biology Workshop*. Utah State Univ., Logan, Utah.
- DORF, E. 1936. A late Tertiary flora from southwestern Idaho. *Publ. Carnegie Inst. Wash.* 476: 73-124.
- . 1942. Upper Cretaceous floras of the Rocky Mountain region. *Publ. Carnegie Inst. Wash.* 508: 1-168.
- EDWARDS, S. W. 1983. Cenozoic History of Alaskan and Port Orford *Chamaecyparis* Cedars. Ph.D. Dissertation. Univ. California, Berkeley, California.
- ENGLER, A. 1879. Versuch einer Entwicklungsgeschichte der extratropischen Florengebiete der nördlichen Hemisphäre. Wilhelm Engelmann, Leipzig.
- FIELDS, P. F. 1983. A Review of the Miocene Stratigraphy of Southwestern Idaho, with Emphasis on the Payette Formation and Associated Floras. M.A. Dissertation. Univ. California, Berkeley, California.
- FRANKLIN, J. S. & C. T. DYRNESS. 1969. Vegetation of Oregon and Washington. *U.S. Forest Service Res. Pap.* PNW-80.
- GRAHAM, A. 1964. The Sucker Creek and Trout Creek Miocene floras of southeastern Oregon. *Kent State Univ. Bull.* 53: 1-147.
- GRANDE, L. 1985. The use of paleontology in systematics and biogeography, and a time control refinement for historical biogeography. *Paleobiology* 11: 234-243.
- HABECK, J. R. 1987 [1988]. Present-day vegetation in the northern Rocky Mountains. *Ann. Missouri Bot. Gard.* 74: 804-840.
- HENNIG, W. 1966. *Phylogenetic Systematics*. Univ. Illinois Press, Urbana, Illinois.
- HICKEY, L. J. 1981. Land plant evidence compatible with gradual, not catastrophic, change at the end of the Cretaceous. *Nature* 292: 529-531.
- . 1984. Change in the angiosperm flora across the Cretaceous-Tertiary boundary. Pp. 279-337 *in* W. A. Berggren & J. A. Van Couvering (editors), *Catastrophes and Earth History*. Princeton Univ. Press, Princeton, New Jersey.
- HOLLICK, A. 1927. The flora of the St. Eugene Silts, Kootenay Valley, British Columbia. *Mem. New York Bot. Gard.* 7: 389-464.

- HOPKINS, D. M., J. V. MATTHEWS, J. A. WOLFE & M. L. SILBERMAN. 1971. A Pliocene flora and insect fauna from the Bering Straight region. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 9: 211–231.
- HOTTON, C. 1984. Palynofloral changes across the Cretaceous–Tertiary boundary in east central Montana, U.S.A. Abstracts Sixth Intl. Palyn. Conf. (Calgary), 66.
- KNOWLTON, F. H. 1904. Fossil plants from Kukak Bay, Alaska. *Harriman Alaska Exped.* 4: 149–162.
- . 1926. Flora of the Luta Formation of Spokane, Washington, and Coeur d'Alene, Idaho. U.S. Geol. Surv. Prof. Pap. 140-A: 17–81.
- LAKHANPAL, R. N. 1958. The Rujada flora of west central Oregon. *Univ. Calif. Publ. Geol. Sci.* 35: 1–66.
- LAMOTTE, R. S. 1935. An upper Oligocene florule from Vancouver Island. *Publ. Carnegie Inst. Wash.* 455: 49–56.
- . 1936. The Upper Cedarville flora of northwestern Nevada and adjacent California. *Publ. Carnegie Inst. Wash.* 455: 57–142.
- LATHRAM, E. H., J. S. POMEROY, H. C. BERG & R. A. LONEY. 1965. Reconnaissance geology of Admiralty Island, Alaska. U.S. Geol. Surv. Bull. 1181-R: R1–R48.
- LEOPOLD, E. B. & M. F. DENTON. 1987 [1988]. Comparative age of grassland and steppe east and west of the northern Rocky Mountains. *Ann. Missouri Bot. Gard.* 74: 841–867.
- & H. D. MACGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pp. 147–200 in A. Graham (editor), *Floristics and Paleofloristics of Asia and Eastern North America*. Elsevier Publ. Co., Amsterdam.
- MCCLAMMER, J. U., JR. 1978. Paleobotany and Stratigraphy of the Yaquina Flora (Latest Oligocene–Earliest Miocene) of Western Oregon. M.A. Dissertation. Univ. Maryland, College Park, Maryland.
- MACGINITIE, H. D. 1933. The Trout Creek flora of southeastern Oregon. *Publ. Carnegie Inst. Wash.* 416: 21–68.
- . 1953. Fossil plants of the Florissant beds, Colorado. *Publ. Carnegie Inst. Wash.* 599: 1–198.
- . 1962. The Kilgore flora. *Univ. Calif. Publ. Geol. Sci.* 35: 67–158.
- . 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *Univ. Calif. Publ. Geol. Sci.* 83: 1–140.
- MANCHESTER, S. R. 1987. The fossil history of Juglandaceae. *Monogr. Syst. Bot. Missouri Bot. Gard.* 21: 1–137.
- MEYER, H. 1973. The Oligocene Lyons flora of northwestern Oregon. *Ore Bin* 35: 37–51.
- MILLER, C. N., JR. 1987 [1988]. Land plants of the northern Rocky Mountains before the appearance of flowering plants. *Ann. Missouri Bot. Gard.* 74: 692–706.
- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev. Biol. Proc. Cambridge Philos. Soc.* 45: 417–450.
- . 1981. Fossil pollen records of extant angiosperms. *Bot. Rev. (Lancaster)* 47: 1–142.
- NICHOLS, D. J. & H. L. OTT. 1978. Biostratigraphy and evolution of the *Momipites–Caryapollenites* lineage in the early Tertiary in the Wind River Basin, Wyoming. *Palynology* 2: 93–112.
- PEARSON, C. P. 1972. A Late Tertiary Florule from the Douglass Creek Basin, Western Montana. M.A. Dissertation. Univ. Montana, Missoula.
- PEARSON, R. C. & J. D. OBRADOVICH. 1977. Eocene rocks in northeastern Washington—radiometric ages and correlation. U.S. Geol. Surv. Bull. 1433: 1–41.
- PLATNICK, N. I. & G. NELSON. 1978. A method of analysis for historical biogeography. *Syst. Zool.* 27: 1–16.
- RICHARDS, P. W. 1952. *The Tropical Rain Forest*. Cambridge Univ. Press, Cambridge.
- SAVIN, S. M. 1977. The history of the earth's surface temperature during the past 100 million years. *Annual Rev. Earth Planet. Sci.* 5: 319–355.
- SKVORTSOV, A. K. 1968. Willows of the USSR: a taxonomic and geographic revision. *Mater. Posnaniyu Fauny Flory SSSR Otd. Bot. vyp.* 15: 5–261. [In Russian.]
- SMILEY, C. J. 1963. The Ellensburg flora of Washington. *Univ. Calif. Publ. Geol. Sci.* 35: 159–267.
- , J. GRAY & L. M. HUGGINS. 1975. Preservation of Miocene fossils in unoxidized lake deposits, Clarkia, Idaho. *J. Paleontol.* 49: 833–844.
- SMITH, H. V. 1941. A Miocene flora from Thorn Creek, Idaho. *Amer. Midl. Naturalist* 25: 473–522.
- SPICER, R. A. & J. T. PARRISH. 1986. Paleobotanical evidence for cool North Polar climates in middle Cretaceous (Albian–Cenomanian) time. *Geology* 14: 703–706.
- , J. A. WOLFE & D. J. NICHOLS. 1987. Alaskan Cretaceous–Tertiary floras and Arctic origins. *Paleobiology* 13: 73–83.
- TSCHUDY, R. H., & TSCHUDY, B. D. 1986. Extinction and survival of plant life following the Cretaceous–Tertiary boundary event, Western Interior, North America. *Geology* 14: 667–670.
- , C. L. PILLMORE, C. J. ORTH, J. S. GILMORE & J. D. KNIGHT. 1984. Disruption of the terrestrial plant ecosystem at the Cretaceous–Tertiary boundary, Western Interior. *Science* 225: 1030–1032.
- UPCHURCH, G. R., JR. & J. A. WOLFE. 1987. Mid-Cretaceous to early Tertiary vegetation and climate: evidence from fossil leaves and wood. Pp. 75–105 in E. M. Friis, W. B. Chaloner & P. R. Crane (editors), *The Origins of Angiosperms and Their Biological Consequences*. Cambridge Univ. Press, Cambridge.
- WAHRHAFTIG, C., J. A. WOLFE, E. B. LEOPOLD & M. A. LANPHERE. 1969. The coal-bearing group in the Nenana coal field, Alaska. U.S. Geol. Surv. Bull. 1274-D: D1–D30.
- WANG, C. W. 1961. *The forests of China*. Harvard Univ. Maria Moors Cabot Found. Pub. 5: 1–313.
- WING, S. L. 1981. A Study of Paleocology and Paleobotany in the Willwood Formation (Early Eocene, Wyoming). Ph.D. Dissertation. Yale Univ., New Haven, Connecticut.
- . 1987 [1988]. Eocene and Oligocene floras and vegetation of the Rocky Mountains. *Ann. Missouri Bot. Gard.* 74: 748–784.
- WOLFE, J. A. 1964. Miocene floras from Fingerrock

- Wash, southwestern Nevada. U.S. Geol. Surv. Prof. Pap. 454-N: N1-N36.
- . 1966. Tertiary plants from the Cook Inlet region, Alaska. U.S. Geol. Surv. Prof. Pap. 398-B: B1-B32.
- . 1969. Neogene floristic and vegetational history of the Pacific Northwest. *Madroño* 20: 83-110.
- . 1972. An interpretation of Alaskan Tertiary floras. Pp. 201-233 in A. Graham (editor), *Floristics and Paleofloristics of Asia and Eastern North America*. Elsevier Publ. Co., Amsterdam.
- . 1977. Paleogene floras from the Gulf of Alaska region. U.S. Geol. Surv. Prof. Pap. 997: 1-108.
- . 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Amer. Sci.* 66: 694-703.
- . 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. U.S. Geol. Surv. Prof. Pap. 1106: 1-37.
- . 1981a. Paleoclimatic significance of the Oligocene and Neogene floras of northwestern United States. Pp. 79-101 in K. J. Niklas (editor), *Paleobotany, Paleoecology, and Evolution, Volume II*. Praeger Publishers, New York.
- . 1981b. Vicariance biogeography of the angiosperms in relation to paleobotanical data. Pp. 413-435 in G. Nelson & D. E. Rosen (editors), *Vicariance Biogeography: A Critique*. Columbia Univ. Press, New York.
- . 1985. Distribution of major vegetational types during the Tertiary. Pp. 357-375 in E. T. Sundquist & W. S. Broecker (editors), *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archaean to Present*. Amer. Geophys. Union Geophys. Monogr. 32, Washington, D.C.
- . 1987. Late Cretaceous-Cenozoic history of deciduousness and the terminal Cretaceous event. *Paleobiology* 13: 215-226.
- & R. Z. POORE. 1982. Tertiary marine and nonmarine climatic trends. Pp. 154-158 in W. Berger & J. C. Crowell (editors), *Climate in Earth History*. Natl. Acad. Sci. Studies in Geophysics, Washington, D.C.
- & T. TANAI. 1980. The Miocene Seldovia Point flora from the Kenai Group, Alaska. U.S. Geol. Surv. Prof. Pap. 1105.
- & ———. 1987. Systematics, phylogeny, and distribution of *Acer* (maples) in the Cenozoic of western North America. *J. Fac. Sci. Hokkaido Imp. Univ., Ser. 4, Geol.* 22: 1-246.
- & G. R. UPCHURCH, JR. 1986. Vegetation, climatic and floral changes at the Cretaceous-Tertiary boundary. *Nature* 324: 148-152.
- & ———. 1987a. Leaf assemblages across the Cretaceous-Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proc. U.S. Natl. Acad. Sci.* 84: 5096-5100.
- & ———. 1987b. North American nonmarine climates and vegetation during the Late Cretaceous. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 61: 33-78.
- & W. WEHR. 1987. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. U.S. Geol. Surv. Bull. 1597: 1-25.
- , D. M. HOPKINS & E. B. LEOPOLD. 1966. Tertiary stratigraphy and paleobotany of the Cook Inlet region, Alaska. U.S. Geol. Surv. Prof. Pap. 398-A: A1-A29.